New apes fill the gap

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The relative abundance of Eurasian apes between 12.5 and 8 Ma—in contrast to a dearth of African apes during the same chronologic interval—has led some investigators (1, 2) to suggest that the African ape–human clade evolved from a Eurasian ancestor, specifically, a previously undescribed and unnamed ape from Turkey (3). In the last several weeks, three new ape genera have been reported, one from Turkey (*Ouranopithecus turkae*), one from Ethiopia (*Chororapithecus abyssinicus*), and the latest, *Nakalipithecus nakayamai*, from Kenya, which is the subject of the article by Kunimatsu *et al.* (4) in a recent issue of PNAS.

Filling the Gap

N. nakayamai is described as a large ape, the size of a female gorilla, dating 9.9–9.8 Ma. Its dentognathic morphology includes thick-enameled molars, a thickened mandibular body, and a low-crowned upper canine that is as broad as it is long. In these features, *N. nakayamai* most closely resembles the slightly younger 9.6- to 8.7-Ma Greek ape *Ouranopithecus macedoniensis* (5–7). The Turkish ape, *O. turkae*, is the youngest, with a biochronological placement of 8.7–7.4 Ma (8). The dental morphology of *Nakalipithecus* and of the two *Ouranopithecus* species suggests hard-object frugivory and, together with their large sizes, implies terrestrial foraging for at least a portion of their niche-space.

The apparent 14- to 7-Ma African "ape gap" (9) is now populated not only by *Nakalipithecus* but also by the penecontemporaneous Kenyan large ape *Samburupithecus kiptalami* (10), dated slightly younger at 9.6 Ma (11, 12), and by yet another large gorilla-like ape, *C. abyssinicus*, from the 10.5- to 10-Ma horizons of Chorora, Ethiopia (13). Additional isolated, but important, large ape remains from Ngorora, Kenya, localities believed to be ≈12.5 Ma (14) may evidence even greater species diversity. Did the African ape–human clade arise in Africa, after all? Some think so (9, 15–17). Where there was once a wide gap, we are now provided with a substantial intra-African great ape diversity in the 12.5- to 9.6-Ma interval.

Nakalipithecus, *Samburupithecus*, and *Chororapithecus* lived in Africa's rifts at a time of sweeping paleoclimatic, faunal, and floral evolution in Western Eurasia and Africa: a change from tropical and subtropical forested conditions to more open-country, seasonal conditions. In Eurasia, this change is recorded as the so-called Pikermian biome (18), when large mammal faunas with the diverse lineages of horses, antelopes, giraffes, rhinoceroses, and distant relatives of elephants evolved and extended their geographic ranges from Spain to China between 8 and 5 Ma. The origins of this community are not well understood, but the Sinap fauna in Turkey records their earliest occurrence ≈10.6–9.7 Ma (19). The Late Miocene of Africa records a cohort of these Pikermian taxa as immigrants into northern and eastern Africa ≈8 Ma, including species of mustelids, hyaenids, felids, horses, giraffes, and antelopes (17). Few large mammals exited Africa at this time, but *Nakalipithecus*, being older and more primitive than its reported descendent *Ouranopithecus*, is a plausible candidate for this distinction. It is not surprising that Kunimatsu *et al.* (4) report here that the associated paleoenvironments of *Nakalipithecus* and *Samburupithecus* are similar to the seasonal, sclerophyllous evergeen woodlands of the Pikermian biome (20).

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Origin of the African Ape–Human Clade

Why the radical shift in scientific opinion from the out-of-Europe view to a plausible African origin of the African ape–human clade? In a poignant short essay on the subject, Hill (9) has reported a simple, yet important, set of facts: "Africa is approximately 4,554,123.6 square kilometers in area, but nearly all of the relevant sites could be grouped in a box a few hundred miles on each side. So when people talk about fossil apes or hominins in 'Africa' they are really talking about fossil apes or hominins from an area about 0.1% of the African continent as a whole." Cote (21) has demonstrated that the abundance of fossil ape remains in Eurasia,—compared with a dearth of similar-aged apes in Africa—is due to sampling: Eurasian localities are much richer and more diverse during this interval than African localities, and hence their apes are better represented. Africa has yielded the oldest and most diverse Miocene–Pliocene hominoids. It is the only continent where the chimp and gorilla live in the wild, and it has the earliest bona fide hominid *sensu stricto* remains. Moreover, there is no evidence of a mass ape extinction at the end of the Middle Miocene, nor is it likely that a Eurasian species founded the African ape–human clade as the result of a biogeographic retreat from Eurasia (1). What the science of biogeography relentlessly teaches us is that species extend their ranges when geographic and paleoenvironmental circumstances allow it: nothing more, nothing less.

Japanese paleoanthropology is a relatively small field, with few researchers compared with North American, European, and African research schools. So it is remarkable that the two Japanese human-origins research teams—one working with Ethiopian counterparts at Chorora, Ethiopia, and the other working in the Samburu Hills and Nakali, Kenya—have made three of the most exciting and important East African ape discoveries in the last few years. All three of these sites were previously investigated by multiple research teams that found no ape fossils at these localities. It is imperative to acknowledge that these recent discoveries occurred only because of the expertise, tenacity, and hard work of these scientists. Our hats are off to them.

Darwin taught us that imperfections of the geological record should not be overinterpreted as biological signal. These new discoveries show that gaps are best filled the old-fashioned way. But beyond the gap-filling foreseen by Darwin, paleobiologists are now blessed with extensive new

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toolkits with which to unlock ancient evolutionary histories. We can now achieve chronological positioning of continental fossil localities beyond our wildest dreams of 40 years ago. The possibility of correlating paleoenvironmental signals recorded in deep ocean cores with those in terrestrial lake systems allows exciting new testable hypotheses about the relationships between environmental change and biotic community response. Molecular studies continue to provide robust hypotheses of ape–human divergence dates. However, it is new fossil discoveries, such as that described by Kunimatsu *et al.* (4), that promise to provide us with the most essential data about human origins and give us new insights into when, where, how, and under what circumstances the African ape–human clade evolved. Expanded paleontological exploration, founded in sound collection, conservation, documentation, analysis, and reporting of whole biotic communities, coupled with the development of secure geologic contexts, are all essential elements of the continued quest to discover our origins.

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